

REVIEW

## Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem

Shahid Naeem\* and  
Justin P. Wright  
Department of Zoology,  
University of Washington,  
24 Kincaid Hall, Seattle,  
WA 98195, USA  
\*Correspondence: E-mail:  
naeems@u.washington.edu

### Abstract

Experimental investigations of the relationship between biodiversity and ecosystem functioning (BEF) directly manipulate diversity then monitor ecosystem response to the manipulation. While these studies have generally confirmed the importance of biodiversity to the functioning of ecosystems, their broader significance has been difficult to interpret. The main reasons for this difficulty concern the small scales of the experiment, a bias towards plants and grasslands, and most importantly a general lack of clarity in terms of what attributes of functional diversity (FD) were actually manipulated. We review how functional traits, functional groups, and the relationship between functional and taxonomic diversity have been used in current BEF research. Several points emerged from our review. First, it is critical to distinguish between response and effect functional traits when quantifying or manipulating FD. Second, although it is widely done, using trophic position as a functional group designator does not fit the effect-response trait division needed in BEF research. Third, determining a general relationship between taxonomic and FD is neither necessary nor desirable in BEF research. Fourth, fundamental principles in community and biogeographical ecology that have been largely ignored in BEF research could serve to dramatically improve the scope and predictive capabilities of BEF research. We suggest that distinguishing between functional response traits and functional effect traits both in combinatorial manipulations of biodiversity and in descriptive studies of BEF could markedly improve the power of such studies. We construct a possible framework for predictive, broad-scale BEF research that requires integrating functional, community, biogeographical, and ecosystem ecology with taxonomy.

### Keywords

Biodiversity, biogeography, ecosystem functioning, functional groups, research framework.

*Ecology Letters* (2003) 6: 567–579

### INTRODUCTION

The study of the ecosystem consequences of biodiversity loss represents a synthetic field of ecological research that seeks to understand how changes in species composition, distribution, and abundance alter ecosystem functioning (Schulze & Mooney 1993; Kinzig *et al.* 2002; Loreau *et al.* 2002b; Naeem 2002c). In this work, ecosystem functioning refers specifically to biogeochemical activities, such as production, community respiration, decomposition, nutrient cycling, or nutrient retention. As changes in biodiversity are widespread, findings from this research have received considerable attention (Naeem *et al.* 1994; Hooper &

Vitousek 1997; Naeem & Li 1997; Tilman *et al.* 1997; Wardle *et al.* 1997; Hector *et al.* 1999; Sankaran & McNaughton 1999; Emmerson *et al.* 2001; Engelhardt & Ritchie 2001; Paine 2002; Pfisterer & Schmid 2002), but these findings have been and continue to be difficult to interpret (Guterman 2000; Kaiser 2000; Naeem 2002a). Synthesis and consensus are emerging, however, and the central challenges are being identified (Hughes & Petchey 2001; Loreau & Hector 2001; Loreau *et al.* 2002b) for biodiversity and ecosystem functioning (BEF) research to become a predictive science. The question for BEF research is no longer whether biodiversity matters, but how it matters (Rosenfeld 2002).

The functioning of an ecosystem, however, is not governed by the phylogenetic content of its biota, but by the functional traits of individuals, the distribution and abundance of these individuals, and their biological activity. Here, we restrict the term “functional trait” to a specific character or phenotypic trait of a species that is associated with a biogeochemical process or ecosystem property under investigation. Since BEF’s beginning in the early 1990s, the majority of BEF studies have dealt with functional diversity (FD) indirectly by employing combinatorial experimental designs that manipulate taxonomic diversity (TD) of a predefined species pool selected to represent the range of functional types found in the ecosystem under investigation. By functional types we mean individuals or species that possess a common set of functional traits selected by the investigator. In BEF research, a combinatorial experiment is one in which the investigator selects species at random from the predefined species pool and constructs numerous combinations of species ranging from high to low species richness, producing a gradient in TD to explore how ecosystem functioning responds to variation in biodiversity (Naeem 2002a).

In principal, this combinatorial approach seems appropriate, but it has prevented extrapolation from species-based experimental findings much beyond confirming that biodiversity matters. This limitation arises in part because it has been difficult to distinguish between results due to an increasing probability that a single species with extraordinary functional attributes is present in higher diversity communities (e.g. sampling) from results due to the possibility that increasing diversity increases the probability of including species that have complementary functional traits (e.g. complementarity) (Huston 1997; Hector 1998; Lepš *et al.* 2001; Loreau & Hector 2001). Clearly, better knowledge about functional traits could help resolve such difficulties.

Recognition of the importance of functional traits has led BEF studies to explicitly examine FD rather than implicitly examining it by using a combinatorial design based on combinations of functional groups rather than species (Hooper & Vitousek 1997; McGrady-Steed *et al.* 1997; Naeem & Li 1997; Van der Heijden *et al.* 1998; Hector *et al.* 1999; Mulder *et al.* 1999; Naeem *et al.* 1999; Petchy *et al.* 1999; McGrady-Steed & Morin 2000; Wardle *et al.* 2000; Engelhardt & Ritchie 2001; Downing & Liebold 2002; Naeem 2002b; Paine 2002). These studies have provided important insights into the role FD plays in ecosystem functioning. These function-based studies, however, like their species-based counterparts, have also been limited to a confirmatory role in the sense that beyond confirming that FD matters, it remains unclear what mechanism or mechanisms are responsible for biodiversity effects where they have occurred.

The focus of this review is to provide an overview of our current understanding of how FD is used in BEF research. We are specifically concerned with the implications of FD

for expanding BEF research to address larger scale issues in biodiversity and global change research. In particular, we are interested in understanding how different kinds of environmental change, or environmental drivers, cause changes in biodiversity that in turn affects ecosystem functioning at landscape levels. We will refer to this expanded program in BEF as *broad-scale BEF research*. Our review is therefore a critique of ongoing approaches and the presentation of an idea for a synthetic framework.

We have selected three critical issues; (1) the role of species traits in ecosystem functioning, (2) the distribution of functional traits in species assemblages, and (3) proposing a framework for broad-scale BEF research that incorporates trait-based FD in a way that can transform BEF from a confirmatory to a predictive science.

The issue of a framework for broad-scale BEF research is central to our review. Given the complexities and controversies surrounding BEF research, it would seem that to expand the science to address even larger scale issues would require tackling seemingly insurmountable problems. The only way to know for sure what the limitations may or may not be for BEF research is to develop a hypothetical framework within which we can explore what is necessary to achieve an expansion of small-scale BEF to broad-scale BEF research.

In this proposed framework, we introduce the possibilities of using biotic inventories, phylogenies, and biogeographic methods for expanding BEF’s scale of inference and improving its predictive power. Here, biotic inventories refer to taxonomic information available about a biota independent of information about the ecology or relative abundance of the species within the inventory. Biogeographic methods refer to the use of extrinsic or abiotic covariates of biodiversity (e.g. latitude, potential evapotranspiration, disturbance regimes and other non-community or non-population factors) to predict distribution and abundance.

## FUNCTIONAL TRAITS AND ECOSYSTEM FUNCTIONING

### Current biodiversity research

Much of contemporary biodiversity research (e.g. Wilson 1988; Groombridge 1992; Hawksworth 1995; Reaka-Kudla *et al.* 1997; Groombridge & Jenkins 2000) does not concern itself with ecosystem functioning or functional traits. Rather, its emphasis has been on TD, i.e. the richness (number of species) and evenness (relative abundance) of assemblages (e.g. Magurran 1988; Colwell & Coddington 1995; May 1995), cumulative phylogenetic distance among species (e.g. Vane-Wright *et al.* 1991; Warwick & Clarke 1995), and spatial and temporal patterns in the distribution of species within a biota (MacArthur 1972; Brown 1995; Rosenzweig 1995; Gaston 2000). The identification of species groups in

this approach involves hierarchical clustering methods based on phylogenetic distances among individuals. Note that information used in taxonomic classification schemes, although often based on traits, is independent of the functional significance of the traits species possess.

In contrast, in BEF research, FD is likely to be more relevant than TD or richness and evenness. Information on the relative abundance of individuals, their functional traits, and their activity, is vital because how a biota affects the functioning of the ecosystem within which it resides is very much a function of these factors. Indeed, debates surrounding BEF research concern issues of distribution and abundance such as so called “hidden treatment” effects or sampling (Huston 1997) or the fact that in most communities, the majority of species are rare while only a few are abundant in contrast to the initially uniform distributions of species in experimental research (Schwartz *et al.* 2000). Effective BEF research must address distribution and abundance (Wilsey & Polley 2002).

At first it might appear ideal if FD could be quantified by hierarchical clustering methods similar to those used in TD, using inter-specific distances in trait space rather than phylogenetic distance (Walker *et al.* 1999; Petchey & Gaston 2002). We will argue, however, that indiscriminate, trait-based measures of FD are not necessarily useful to broad-scale BEF research.

### The importance of traits

Identifying the key traits that influence particular ecosystem functions is an important step in understanding how biodiversity affects ecosystem function, and there is a long history of such research. The exact traits responsible for governing a given ecosystem function will vary depending on numerous factors including temperature, soil or water conditions, precipitation, nutrient availability, and time since disturbance. In many cases, traits important in determining a given ecosystem function may be shared among multiple species in an assemblage. Given this redundancy of trait distribution, there has been a long history of attempts to classify species with similar traits into functional groups.

As reviews of functional groups have noted, however, there are many obstacles to developing effective functional classification schemes. Some traits may only be expressed by one or a few species in an assemblage, and some species may have bundles of traits that are unique, defying classification into *a priori* functional groups. Furthermore, some species may express certain functional traits in one context or at one life stage and other traits at other times or under different conditions. For example, whether or not nitrogen-fixing microbes actually fix nitrogen depends on numerous conditions, and the functional role of a tree seedling in the understory is quite different in most respects

from the role of a canopy tree of the same species. The presence of species that defy clean categorization or that shift traits is a significant challenge to classifying assemblages into functional groups.

Nevertheless, there are a few generalizations that can be made. For example, traits that affect carbon acquisition and processing pathways are likely to be key determinants of ecosystem functions such as primary and secondary productivity, decomposition rates and nutrient cycling. Likewise, traits that determine nutrient and water use and recycling pathways are likely to interact with traits affecting carbon use to control most ecosystem functions. As in most of the ecological sciences, such generalizations permit developing appropriate theories and methods.

### Response versus effect-functional traits

Functional classification schemes vary significantly from one another in how they group species by functional traits. Several recent reviews on functional groups provide considerable coverage of the many issues surrounding the identification of functional groups, especially for plants (Smith *et al.* 1997; Diaz & Cabido 2001; Hooper *et al.* 2002; Lavorel & Garnier 2002).

Perhaps the single most important issue arising from these reviews is that functional traits should be separated into effect functional traits (or simply, effect traits) and response functional traits (or simply, response traits) (Hooper *et al.* 2002; Lavorel & Garnier 2002). Effect traits contribute to the function being measured. For example, if total soil nitrogen is the ecosystem function of interest, then within a soil microbial community traits associated with denitrification, nitrification, ammonification, or any other part of the nitrogen cycle represent effect traits. Response traits, on the other hand, determine the response of the species to an environmental change. For example, in the face of a drought (i.e. an environmental change), traits associated with drought tolerance or susceptibility of soil microbes to lowered soil moisture are response traits. With respect to BEF research, response functional traits are likely to be most important in determining the stability and resilience of biota following perturbations. Note that response and effect as used here in reference to functional traits, should not be confused with other usages, such as the response to or effect of a perturbation on ecosystem functioning or the response to or effect of a biotic factor on a population, such as competition.

### A survey of functional classification schemes

Developing effective strategies for the classification, quantification and manipulation of function-based diversity is an

important step in BEF research. Unfortunately, there is little concordance among the many approaches used to develop functional classification schemes (Gitay & Noble 1997). Gitay & Noble (1997) identify three major types of functional classification schemes; (1) subjective, (2) deductive, and (3) data-defined. An example of the subjective approach is that of Bisevac & Majer (1999) who clustered 96 ant species from 30 genera into seven functional groups based loosely on known or presumed biotic interactions and niches. These groups were; (1) dominant Dolichoderinae, subordinate Camponotini, (2) climate specialists (subgroups were hot, cold, and tropical), (3) cryptic species, (4) opportunists, (5) generalized Myrmicinae, and (6) specialist predators. They used these groupings to demonstrate that the ant assemblage in control sites differed in its functional composition from sites undergoing restoration following mining. Note that this scheme mixes taxonomic (e.g. group 1), response trait (e.g. group 2), life history (e.g. group 4), and trophic (e.g. group 6) groups.

An example of a deductive method is that of Huston & Smith (1987) in which the authors deduced five functional traits of plants important in succession based on their individual-based model of succession. These plant traits were: (1) maximum size, (2) maximum growth rate, (3) maximum longevity, (4) maximum rate of sapling growth, and (5) shade tolerance. In their simulations, there were 32 possible plant functional types with two levels assigned to each of five traits. As the authors note, one has to be careful using this method because depending on the number of traits and the number of levels assigned, one could have more functional types than there are species or construct biologically implausible functional types (e.g. a large, fast-growing, long-lived, shade-tolerant, slow-sapling growth tree species).

Finally, an example of data-defined functional groups (also "emergent" functional groups, Lavorel *et al.* 1997) is that of Kindscher & Wells (1995) who used discriminant-function and detrended-correspondence analyses applied to ecophysiological traits to test for significant segregation of 203 prairie grassland plant species into eight functional groups. These were: (1) C4 grasses; (2) C3 grasses and sedges; (3) annuals and biennial forbs; (4) ephemeral spring forbs; (5) spring forbs; (6) summer/fall forbs; (7) legumes; and (8) woody shrubs.

In some cases, one set of functional groups may be based on another. For example, Steneck & Watling (1982) defined seven functional groups of algae (micro-, filamentous, foliose, articulated calcareous, and crustose coralline algae as well as corticated and leathery macrophytes) from which four functional groups of herbivorous mollusks were devised (rhipidoglossan-, taenioglossan-, docoglossan-, and polyplacophoran). These groups were based on the structure and function of the mollusk radula, (the equivalent of "teeth"), that determined which algal functional groups they could eat.

### Functional classification appropriate for BEF

As one can see even from this small set of examples, functions are often defined operationally, leading to an enormous array of seemingly eclectic classification schemes. When faced with such apparent eclecticism, data-defined functional groups may appear objective and therefore preferable to subjective or deductive ones (Petchey & Gaston 2002), but the selection of traits in data-defined functional groups can often predetermine the outcome, thus a data-defined functional scheme is not necessarily objective. Theoretically, as one increases the number of traits used in the analysis to the point where the relevant effect and response traits become only a minority of the traits being used to define groups, the pattern of clustering among such an "objective" or neutral set of traits should converge on the taxonomic pattern of clustering. Thus, one must be careful not to include large numbers of neutral traits in data-defined classification schemes in order to avoid spurious correlations between TD and FD. More importantly, a functional classification scheme in which TD and FD are highly correlated would be of little utility for BEF research if the functional groups provide no ability to predict how an ecosystem's community would respond to an environmental driver that alters biodiversity and how it's functioning might be affected by this response. Still, careful use of data-defined functional groups provide one avenue for gaining a further understanding of how functional traits are distributed among species and how FD might affect ecosystem functioning (e.g. Craine *et al.* 2002).

Trophic-based functional classification schemes, while useful in many other contexts, are not useful in the context of response-effect, trait-based BEF research. Higher trophic groups primarily influence the distribution and abundance of primary producers and decomposers either through direct consumption or through shifts in the distribution and abundance of prey species. Higher trophic groups may also be important in regulating certain ecosystem functions (e.g. Pastor *et al.* 1993; Huntly 1995) or cycling rates (e.g. Loreau 1994; Loreau 1995; Zheng *et al.* 1997). In such cases, simply classifying organisms based on trophic position is unlikely to be useful. Rather, it is more important to classify species according to their influence on the distribution and abundance of species from a community perspective or on cycling rates from an ecosystem perspective.

As BEF research is based on drivers and ecosystem functions selected by the investigator, the most appropriate functional classification approach is to deduce the relevant effect and response traits and base clustering algorithms on how species in the assemblage share these traits. One would deduce two sets of functional groups: a set of response functional groups and a set of effect functional groups.

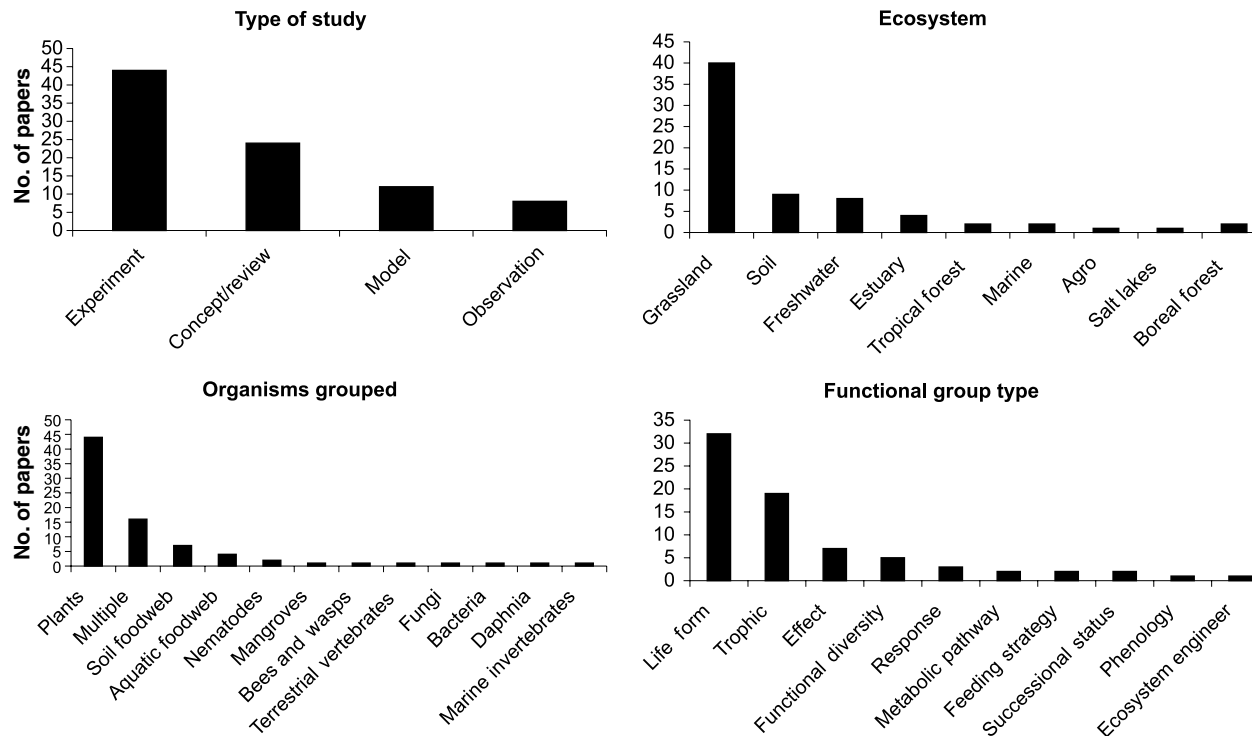


Figure 1 Current trends in functional group literature. See text for details.

### Functional groups as used in current literature

We surveyed published studies that examine the relationship between FD and ecosystem function to determine which approaches are most common and which are potentially of the most use. We searched BIOSIS and the ISI (Institute of Scientific Information) Web of Science Database for papers using the words “function\*,” “group\*,” “diversity,” and “ecosystem” and selected articles that clearly discussed the impact of FD on ecosystem function. While the search was not exhaustive, we identified 91 studies where we could determine the type of study (e.g. experimental or observational), the type of ecosystem studied, the type of organism studied, and the functional classification scheme used.

There was a broad mix of study types with almost half of the studies (44) containing an experimental component (Fig. 1a). However, less than 10% of the studies (8) were observational, making it difficult to compare the results generated in the numerous experimental studies to natural patterns. As with BEF research in general, grasslands represent the most common system for study (Fig. 1b), and relatively few studies are in marine and freshwater ecosystems. Most of the studies were conducted with plants (Fig. 1c), again similar to BEF research in general. Plants, particularly common grassland plant species, are relatively easy to manipulate in experimental settings. The tractability of plant-based studies has therefore led to a bias in BEF

research that markedly constrains its ability to extrapolate to multi-trophic or more complex ecosystems.

A wide variety of schemes were used to classify species according to their functional traits, but subjective schemes were the most common. Over half of the studies classified organisms based on either their life form (typically,  $C_3$ ,  $C_4$ , legume and non-leguminous forbs) or trophic position (Fig. 1d). With the exception of a few studies that calculated some measure of FD within the communities (Folke *et al.* 1996; Walker *et al.* 1999; Norberg *et al.* 2001; Petchey & Gaston 2002), most classification schemes were of a subjective nature. Only a few studies specifically distinguished between effect and response functional groups, and these were exclusively either concept/review papers (Walker 1992; Brussaard *et al.* 1997; Strange *et al.* 1999; Levin *et al.* 2001; Lavorel & Garnier 2002; Rosenfeld 2002) or models (Nijs & Impens 2000; Fonseca & Ganade 2001; Loreau 2001).

### THE DISTRIBUTION OF FUNCTIONAL TRAITS IN SPECIES ASSEMBLAGES

From our survey in the previous section, it is apparent that understanding FD from the standpoint of effect and response traits is central to the transformation of BEF research from a confirmatory to a broad-scale, predictive science. It is also apparent that the majority of work done on FD only points the way for the transformation. The

majority of studies used subjective rather than deduced functional groups, were not response or effect-trait based, and were biased towards plants and grassland ecosystems thereby providing insufficient insights for expanding current BEF research to broader scale issues.

Establishing the distribution of response-effect functional traits in species assemblages, either in natural communities or in the pool of species to be used in an experiment, is a crucial step in BEF research for it to mature to a level where it can address broad-scale issues. This maturation requires developing a framework for deriving the distribution of functional traits in the biota of ecosystems and determining how such distributions govern response and effect. Numerous biotic and abiotic factors affect the composition, distribution, and abundance of species in assemblages that in turn will affect the distribution of functional traits in a community. An additional issue concerns the possibility that even if species are taxonomically distinct or singular, it is possible they may be functionally equivalent or redundant and therefore lumped into one group. Where a species resides in the singularity-redundancy continuum can be important when determining the distribution of functional traits. Here, we consider how current BEF research has dealt with these issues.

### The distribution of traits in current BEF research

BEF research has dealt with the distribution of functional traits by either assuming or ensuring that TD and FD are correlated, then inferring FD from TD. Although many BEF studies manipulated FD, TD, or both, recent BEF reviews have identified a positive association between TD and FD inherent in the design of plant-only experimental studies (Hooper *et al.* 2002; Naeem 2002b; Schmid *et al.* 2002). The observed positive relationship in BEF studies stems in part from functional group richness covarying with taxonomic richness. The functional classification schemes did not permit a single species to belong to more than one functional group whereas a single functional group could include many species (Schmid *et al.* 2002). This positive relationship, as indicated above, also stems from the investigators' attempts to construct species pools that represent a fair sampling of subjectively derived functional groups common to the ecosystem under investigation. Species pools were constructed to have a balanced representation of functional groups and, by the combinatorial design, a set of replicates that fairly sampled the realm of possible community types. Of the studies that simultaneously examined both taxonomic and FD, the relationship between FD and ecosystem functioning has proven to be a significant predictor of ecosystem functioning, in some cases explaining a higher amount of the variance in ecosystem functioning than species richness by itself (Tilman *et al.* 1997; Hector *et al.* 1999; Naeem *et al.*

1999). Beyond experiments such as these that simultaneously varied TD and FD, BEF experimental studies have been fairly limited in their exploration of FD.

### Redundancy, singularity and the distribution of traits

Grouping species by function automatically infers a degree of functional redundancy or equivalency of traits among species (Walker 1992; Gitay *et al.* 1996; Naeem 1998; Diaz & Cabido 2001; Wellnitz & Poff 2001). Furthermore, attempts to classify species into distinct groups based on functional traits assume that the traits most relevant to determining ecosystem function are distributed in a discrete rather than continuous fashion (Chapin *et al.* 1996).

If most species exhibit unique traits important in determining ecosystem function (e.g. ecosystem engineering by beaver), the relationship between TD and FD is likely to be strong (Diaz & Cabido 2001), whereas if many species exhibit similar traits (i.e. they are redundant), the TD–FD relationship is likely to be weaker. If key functional traits are distributed in a uniform fashion among species, attempts to classify species into distinct functional groups may inhibit attempts to determine the TD–FD relationship.

### Community processes and BEF

Understanding the forces that control the number and relative abundances of species in an assemblage requires incorporating the role of higher trophic levels, ecosystem engineering, pollination, and other interactions into traditional BEF research.

Several studies have examined what community properties of biodiversity regulate the magnitude and dynamics of ecosystem functioning (e.g. Naeem & Li 1997; Doak *et al.* 1998; Tilman *et al.* 1998; Mulder *et al.* 1999; Yachi & Loreau 1999; Downing & Liebold 2002; Paine 2002; Pfisterer & Schmid 2002), a topic recently reviewed by Loreau *et al.* (2002a) and Hughes *et al.* (2002). Community properties affect the abundance, population dynamics, and activity of primary producers, decomposers, and non-decomposer heterotrophs, such as species composition, the matrix of biotic interactions among species, trophic structure, and ecosystem engineering, and are likely to affect the magnitude and variability of ecosystem functioning.

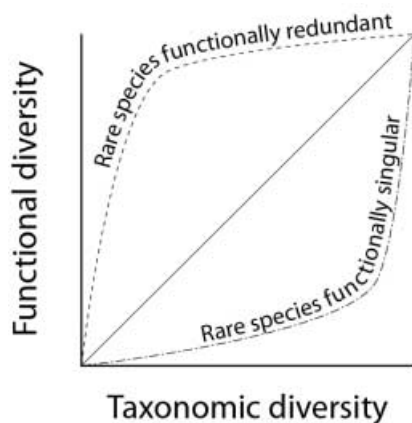
### Biogeographical ecology and BEF

BEF research has focused on local or within-site variation in biodiversity (Naeem 2001; Bengtsson *et al.* 2002; Bond & Chase 2002; Chase & Leibold 2002) and has ignored commonness and rarity (Schwartz *et al.* 2000). The enormous resources required for multi-factorial combinatorial experiments make expansion of experimental BEF research

to address these additional issues prohibitive, but biogeographical ecology may provide some solutions. Biogeographical ecology has identified distinct large-scale patterns in species composition (Brown 1995; Rosenzweig 1995; Gaston 2000; Gering & Crist 2002) and patterns in distribution and abundance (MacArthur 1972; May 1975; Hubbell 2001). For BEF research to apply its findings to larger scales and to more realistic communities, biogeographical ecology provides a number of guidelines and potential tools for estimating the composition, distribution, and abundance of species in local communities.

### The relationship between TD and FD

That species are the repositories for functional traits suggests that one may use estimates of TD as a proxy measure of FD. The influences of community and biogeographical processes, however, strongly limit the utility of such an approach. From the above considerations, it is clear that the relationship between TD and FD is likely to be sensitive to which response and effect traits are being considered, which ecosystem function is under investigation, the degree of redundancy and singularity among species, how biotic interactions and trophic structure modify the magnitude, variability, and dynamics of ecosystem functioning, and how biogeographical factors control species composition, distribution and abundance. Given this sensitivity, the relationship between TD and FD is not likely to be useful for large-scale BEF research. For example, combining redundancy-singularity and rarity-commonness, if species are redundant, then ecosystem functioning would be insensitive to much of their



**Figure 2** The relationship between taxonomic and functional diversity. Three possible relationships are shown. The top (dashed) line shows the relationship when rare species are functionally redundant. The middle, straight line (continuous) shows the relationship when every species contributes to functioning and is equally abundant. The third relationship (bottom, dash-dot) shows the relationship when rare species carry unique functional traits.

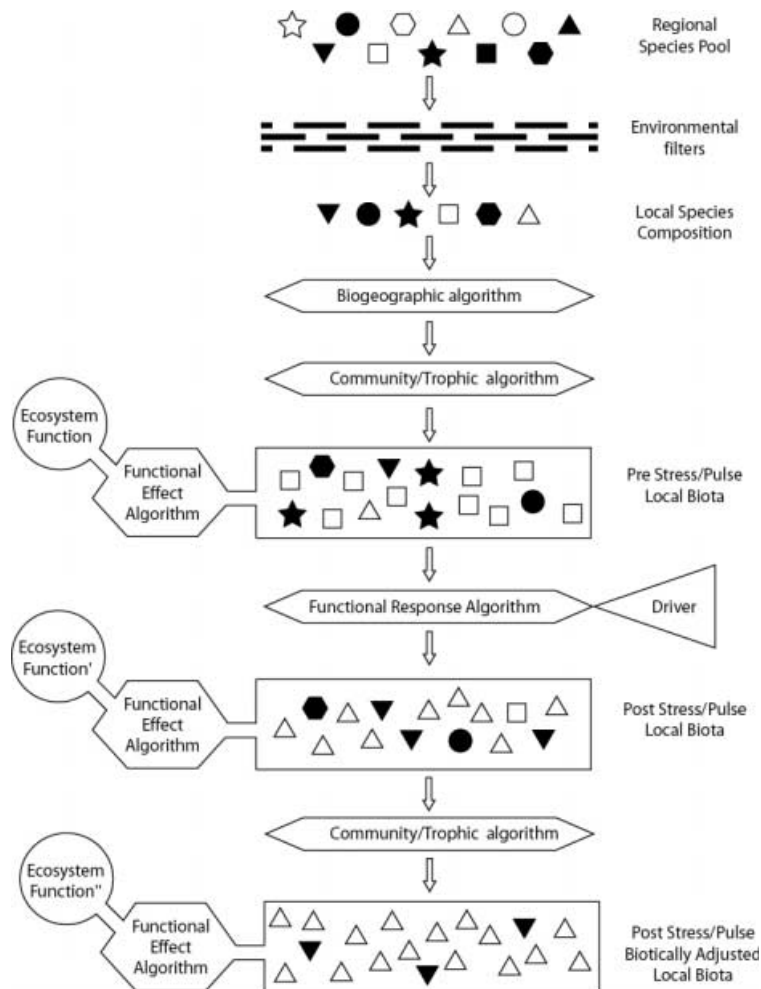
loss, while the converse would be true if rare species were singular. Since redundancy and singularity change as one changes response and effect traits under investigation, the range of possible relationships between TD and FD is enormous (Fig. 2). For this reason, we suggest that attempting to identify a general relationship between TD and FD is likely to be of little utility.

### A FRAMEWORK FOR BROAD-SCALE BEF RESEARCH

From the above considerations, it is clear that what governs the response of an ecosystem to changes in biodiversity is determined by four factors: (1) the species composition of the biota, (2) the abundance of each species, (3) the functional traits each species possess, and (4) the biotic interactions among species that regulate magnitude and variability of expression of the function under investigation. Thus, for a local biota, the regional species pool from which the local biota is constructed consists of a specific set of species that represent the outcome of history, biogeography, and evolutionary processes. As extrinsic or abiotic factors change, such as climate, atmospheric composition, or nutrient inputs and outputs (i.e. what we have been referring to as drivers), species respond to these changes in different ways.

Based on the four factors considered in this review, we suggest the following four-step framework for broad-scale predictive BEF research. Figure 3 provides a schematic outline of this proposed framework. As this is a proposed framework for research that has yet to be conducted, we know of no study that could serve as an example. Rather, we illustrate each part by way of hypothetical examples based on published studies or well-established ecological principles.

- (1) Determine species composition across sites
  - (a) Develop a biotic inventory of the regional species (e.g. species checklists of regions).
  - (b) Determine the local composition of species by applying environmental filter algorithms to regional inventories of species (e.g. use potential evapotranspiration, latitude, elevation, soil fertility, and other abiotic predictors of biodiversity to estimate local compositions). Environmental filters (Woodward & Diament 1991; Keddy 1992) represent the hierarchy of abiotic and biotic factors that constrain the distribution and abundance of species (Diaz *et al.* 1999; Lavorel & Garnier 2002). For example, given a checklist of regional plant species for a habitat in California, high concentrations of magnesium silicate would indicate that only serpentine adapted plants are likely to colonize such areas, thus serpentine soil acts as an environmental filter that selects for species adapted to the conditions specific to such soils. An environmental filter algorithm



**Figure 3** A framework for broad-scale biodiversity and ecosystem functioning research. The top illustrates the regional species pool where each species is represented by a different shape or fill pattern (solid or open). Environmental filters determine the list of species found in the habitat under investigation. Biogeographic algorithms can be used to predict possible patterns of distribution and abundance at equilibrium. A community/trophic algorithm is applied to determine population dynamics, including the presence of keystone species, ecosystem engineers, and where compensatory growth may exist. The final, pre-stress or pre-pulse biota is shown in the first box from the top. Using information about effect functional traits, the magnitude of ecosystem functioning is then predicted (circle to left). To determine dynamics, one must return to the community/trophic algorithm. To predict functioning under stress or pulse type drivers, the community is passed through the functional response algorithm for that particular driver. Note that in the stress or pulse biota (bottom box) the relative abundance of species has changed with the previously rare, open triangle now the dominant species while the species represented by the filled star has gone locally extinct. As a result, ecosystem functioning is expected to change, hence the prime symbol placed in the second ecosystem function circle. For clarity, we have left out feedbacks between ecosystem functioning and the environmental filters and biogeographic algorithms.

would be a set of instructions for selecting species based on biotic and abiotic conditions. Environmental factors can provide powerful means for predicting distribution and abundance. For example, Tuomisto *et al.* (2003) show that 70–75% of the variance in the distribution of melastomes and ferns and fern allies (plants in the family Melastomataceae and pteridophytes, respectively) in Amazonian rainforests can be explained by environmental factors (edaphic factors: pH; loss on ignition;

percentage of clay and silt; and the logarithmically transformed concentration of Ca, K, Mg, Na, and Al, and seasonality). Such analyses suggest that species composition for these plants and perhaps other species that co-occur with them may be predicted over regions by using environmental data.

(2) Determine abundance

- (a) Use biogeographical algorithms to estimate the relative abundance of species. By biogeographical



algorithms we mean a set of instructions by which species distributions may be translated into relative abundance or the commonness and rarity of species (e.g. use biogeographical models such as sequential breakage (Sugihara 1980; Naeem & Hawkins 1994) or neutral models (Hubbell 2001) to estimate relative abundance over the landscape, ensuring that known dominants represent the common species). For example, Belgrano *et al.* (2002) showed strong correlations between plant size and plant density that might be used to predict distribution and abundance of plants given a plant biotic inventory and the mean sizes for plant species in the inventory. Such approaches are necessarily crude approximations, but may nevertheless be useful where data on distribution and abundance are lacking.

- (b) Use biotic interactions (trophic dynamics, competition, presence of ecosystem engineers or mutualists) to understand the variability and range of expression one might expect for ecosystem functioning. For most communities, biotic interactions are seldom known in any detail, but there are instances where the presence or absence of species with strong impacts, such as coral disease agents (Littler & Littler 1995), herbivores (Pastor *et al.* 1993; Zimov *et al.* 1995; Frank & Groffman 1998), ecosystem engineers (Wright *et al.* 2002) or keystone species (Power *et al.* 1996), may at least provide some idea about biotic influences over ecosystem function. Developing more general theory out of these observations will allow us to increase our ability to incorporate species interactions into our prediction algorithms.

### (3) Determine functional traits

- (a) Select a driver of interest that impacts biodiversity (e.g. habitat fragmentation, increased levels of CO<sub>2</sub>, enhanced nitrogen deposition or biological invasion).
- (b) Select an ecosystem function, preferably an ecosystem process associated with biogeochemistry (e.g. decomposition, community respiration, primary production, or nutrient retention).
- (c) Use published natural history or autecological accounts or Integrated Screening Programs to determine the set of relevant functional traits found within the local biota under investigation.
- (d) Establish which response traits are relevant with respect to the selected driver.
- (e) Establish which effect traits are relevant for the selected ecosystem function.

Buchmann *et al.* (1997), e.g. examined  $\delta^{13}\text{C}$  in semi-arid forest vegetation and soil in which stands were differentially

dominated by *Pinus contorta*, *Populus tremuloides*, *Acer negundo* and *Acer grandidentatum*. The vegetation types were considered to be evergreen or deciduous. The influence of these vegetation types were compared with the influences of climate (seasonal patterns in precipitation and temperature), and leaf area index (LAI). In this example, the ecosystem function of interest was carbon flux and emphasis was on ecophysiological mechanisms. While this study did not explicitly concern integrating functional and TD into biodiversity-functioning research, it is a good example of how selecting a function (carbon flux), selecting functional traits relevant to the ecosystem function (ecophysiological traits), and extrinsic (precipitation, temperature) and intrinsic factors (vegetation type, stand structure, LAI), can be integrated.

### (4) Determine ecosystem functioning

- (a) Apply a response algorithm that reconfigures local biota based on driver and response traits.
- (b) Apply a biotic interaction algorithm that reconfigures local biota based on community, trophic, or ecosystem engineer impacts. A biotic interaction algorithm is a set of instructions for modifying distribution and abundance based on interactions. For example, if starfish are present in a marine rocky intertidal community, then mussels would not dominate and herbivore diversity would be higher (Paine 1966).
- (c) Apply an effect algorithm that estimates ecosystem functioning based on changes in biodiversity.

An important challenge that needs to be met for such a framework to be adopted is to establish a precise set of ecosystem functions that should be measured in order to make studies comparable. For example, production is equated with light interception, per cent cover, biomass of clipped strips, and estimates from quadrat or other sampling techniques in terrestrial ecosystems, or biovolume of algae in microcosms. A more precise, universal measure of ecosystem functioning, e.g. could be C assimilation per unit biomass per unit time. While establishing such a set of universal measures and criteria is beyond the purview of this review, we note that early efforts to establish concise terminology, accepted protocol, and universal sets of ecosystem functions and functional traits would represent important first steps.

### A note on the role of biotic/trophic interactions

Note that biotic or trophic interactions come into play in two places in this framework. In each case, they represent factors that modify distribution and abundance; thus they are not part of the functional algorithms. The range of variability in functioning created by trophic interactions would represent

the differences between ecosystem function' and ecosystem function'' (second and third ecosystem function circles from the bottom in Fig. 3). We acknowledge that there are alternative ways of illustrating this and we have left out feedbacks among interacting species to facilitate clarity in our discussion and in Fig. 3.

## SUMMARY AND CONCLUSION

While the functioning of individual ecosystems is the unique result of historical factors, if we hope to predict changes in light of loss of biodiversity, we must begin to look for general patterns. This framework represents just the first steps towards expansion of the BEF approach by considering larger scale patterns of BEF, but the inclusion of historical factors and contingency would be necessary to complete the picture.

The primary motivation for BEF research is to predict the ecosystem significance of widespread changes in biodiversity. While even the earliest empirical and theoretical treatments recognized that functional traits were critical to establishing BEF as a predictive, mechanistic-based science, its reliance on subjectively defined functional groups has yielded a science that has been confirmatory rather than predictive. It has primarily demonstrated that changes in biodiversity, either taxonomic or functional, can alter ecosystem functioning, but it has not provided much insight into why this might be so or how it might apply to large-scale patterns and processes. As our survey shows, functional groups continue to be subjective or data-defined, neither of which serve BEF research very well.

What is needed is to deduce the appropriate set of response and effect traits present in the biota based on, or deduced from the driver and ecosystem function under investigation. Our survey suggests that current efforts have not developed such effect-response, trait-based functional classifications, but progress is being made. It will require a considerable expansion of empirical research in functional ecology, such as Integrated Screening Programs (Diaz & Cabido 2001; Hooper *et al.* 2002), aimed at identifying and classifying species traits. Such programs should focus on classifications that are based on important drivers (e.g. habitat fragmentation, elevated temperature, changes in precipitation, biological invasions, or other drivers that impact biodiversity) and a variety of fundamental ecosystem functions (e.g. production, decomposition, and material and energy flux). Additionally, given the plant bias in current literature (Fig. 1), expansion of this research is especially important for non-grassland plant species and heterotrophic organisms such as decomposers and consumers.

We provide a plausible framework for advancing BEF research that requires synthesizing taxonomy, functional ecology, community ecology, ecosystem ecology, and biogeography. Because all these fields are considerably

well-developed and considerable theory and data exist on these topics, it is possible to attempt a synthetic study using the framework without conducting further research. For example, where plant biotic inventories and ISP-type studies have been conducted, where information on above-ground plant production and relevant climatic, edaphic, and other abiotic factors are available, one could attempt to develop a predictive model of production in relation to vegetation over a region using biogeographical and macroecological principles to estimate vegetation (species composition and relative abundance) in uncharted portions of the region. The utility of the model would be to provide a means by which one could predict the response of regional above ground plant production not only to changes in climatic or edaphic conditions, as is commonly done (e.g. Bazzaz 1990; Chapin *et al.* 1995; Van Minnen *et al.* 2000), but to changes in biodiversity as well. One cannot readily extrapolate results from the current crop of small-scale experiments within which the distribution and abundance of species do not map onto the patterns of distribution and abundance commonly found in nature. For example, in a BEF experiment, legumes and non-legumes are often established with uniform densities, while in many grasslands, legumes are relatively rare. Commonness and rarity have profound implications for ecosystem function and useful BEF models need to account for such factors (Schwartz *et al.* 2000).

On the other hand, to transform BEF from the confirmatory science it has been, conducting combinatorial BEF experiments in which response and effect traits relevant to the ecosystem response under investigation are manipulated, rather than manipulating species richness or subjectively, deductively, or data-derived functional groups, would provide results useful in predicting the specific response of an ecosystem to specific changes in biodiversity. For example, at Cedar Creek, Minnesota, where three key BEF experiments have been conducted (Tilman *et al.* 1996; Tilman *et al.* 1997; Reich *et al.* 2001), designing new combinatorial experiments based on response or effect traits associated with above ground production would provide results that could be employed in developing a predictive model of production for a wide variety of changes in biodiversity. Current findings primarily address random loss of species or random loss of entire functional groups; a fairly limited set of biodiversity changes.

While each part of the framework is based on fundamental principles in ecology, we acknowledge that each part is not without its controversies and alternative theories, but this should not deter attempts to integrate among these currently disparate ecological disciplines. The framework is, at this point, unwieldy and untested, but it emerges from our review as an exciting challenge and a potentially important way forward for BEF research.

## ACKNOWLEDGEMENTS

The authors thank the participants of Adaptive Synthesis Workshop I of the BioMERGE Research Coordinating Network (<http://depts.washington.edu/biomerger/>) for hammering out the initial framework developed here and illustrated in Fig. 3. J. Drake, S. F. Tjossem, O. Schmitz, and E. Bernhardt, and an anonymous reviewer provided critical readings of the manuscript. This work was supported by NSF DEB 0130289.

## REFERENCES

- Bazzaz, F.A. (1990). The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Ann. Rev. Ecol. Systematics*, 21, 167–196.
- Belgrano, A., Allen, P.A., Enquist, B.J. & Gillooly, J.F. (2002). Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecol. Lett.*, 5, 611–613.
- Bengtsson, J., Engelhardt, K., Giller, P., Hobbie, S., Lawrence, D., Levine, J.M. *et al.* (2002). Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. In: *Biodiversity and Ecosystem Functioning: Syntheses and Perspectives* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, pp. 209–220.
- Bisevac, L. & Majer, J.D. (1999). Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. *Restoration Ecol.*, 7, 117–126.
- Bond, E.M. & Chase, J.M. (2002). Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecol. Lett.*, 5, 467–470.
- Brown, J.H. (1995). *Macroecology*. University of Chicago Press, Chicago.
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P. *et al.* (1997). Biodiversity and ecosystem functioning in soil. *Ambio*, 26, 563–570.
- Buchmann, N., Kao, W.-Y. & Ehleringer, J. (1997). Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States. *Oecologia*, 110, 109–119.
- Chapin, F.S., III, Reynolds, H.L., D'Antonio, C.M. & Eckhart, V.M. (1996). The functional role of species in terrestrial ecosystems. In: *Global Change and Terrestrial Ecosystems* (eds Walker, B. & Steffen, W.). Cambridge University Press, Cambridge, pp. 403–430.
- Chapin, F.S., III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995). Response of arctic tundra to experimental and observed changes in climate. *Ecology*, 76, 694–711.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity-biodiversity relationship. *Nature*, 416, 427–430.
- Colwell, R.K. & Coddington, J.A. (1995). Estimating terrestrial biodiversity through extrapolation. In: *Biodiversity Measurement and Estimation* (ed. Hawksworth D.L.). Chapman and Hall, London, pp. 101–119.
- Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funt. Ecol.*, 16, 563–574.
- Diaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
- Diaz, S., Cabido, M. & Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. In: *Ecological Assembly Rules* (eds Weiher, E. & Keddy, P.A.). Cambridge University Press, Cambridge, pp. 338–362.
- Doak, D.F., Bigger, D., Harding-Smith, E., Marvier, M.A., O'Malley, R. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.
- Downing, A.L. & Liebold, M.A. (2002). Ecosystem consequences of species richness and composition in pond food webs. *Nature*, 416, 837–841.
- Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M. & Raffaelli, D.G. (2001). Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature*, 411, 73–77.
- Engelhardt, K.A.M. & Ritchie, M.E. (2001). Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, 411, 687–689.
- Folke, C., Holling, C.S. & Perrings, C. (1996). Biological diversity, ecosystems, and the human scale. *Ecologic. Applic.*, 6, 1018–1024.
- Fonseca, C.R. & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *J. Ecol.*, 89, 118–125.
- Frank, D.A. & Groffman, P.M. (1998). Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology*, 79, 2229–2241.
- Gaston, K. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.
- Gering, J.C. & Crist, T.O. (2002). The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecol. Lett.*, 5, 433–444.
- Gitay, H. & Noble, I.R. (1997). What are functional types and how should we seek them. In: *Plant Functional Types* (eds Smith, T.M., Shugart, H.H. & Woodward, F.I.). Cambridge University Press, Cambridge, pp. 20–46.
- Gitay, H., Wilson, J.B. & Lee, W.G. (1996). Species redundancy: a redundant concept?. *J. Ecol.*, 84, 121–124.
- Groombridge, B. (1992). *Global Biodiversity*. Chapman and Hall, London, United Kingdom.
- Groombridge, B. & Jenkins, M.D. (2000). *Global Biodiversity: Earth's Living Resources in the 21st Century*. World Conservation Press, Cambridge.
- Guterman, L. (2000). Have ecologists oversold biodiversity? Some scientists question experiments on how numerous species help ecosystems. *The Chronicle of Higher Education*, 47, A24–A26.
- Hawksworth, D.L. (1995). *Biodiversity Measurement and Estimation*. Chapman and Hall, London.
- Hector, A. (1998). The effects of diversity on productivity: detecting the role of species complementarity. *Oikos*, 82, 597–599.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G. *et al.* (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hooper, D., Buchmann, N., Degrange, V., Díaz, S.M., Gessner, M., Grime, P. *et al.* (2002). Species diversity, functional diversity and ecosystem functioning. In: *Biodiversity and Ecosystem Functioning* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, pp. 195–208.

- Hooper, D.U. & Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hughes, J.B., Ives, A.R. & Norberg, J. (2002). Do species interactions buffer environmental variation (in theory)? In: *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, pp. 92–101.
- Hughes, J.B. & Petchey, O.L. (2001). Merging perspectives on biodiversity and ecosystem functioning. *Trends Ecol. Evol.*, 16, 222–223.
- Huntly, N. (1995). How important are consumer species to ecosystem functioning? In: *Linking Species and Ecosystems* (eds Jones, C.G. & Lawton, J.H.). Chapman and Hall, New York, pp. 72–83.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Huston, M. & Smith, T. (1987). Plant succession, life history and competition. *Am. Nat.*, 130, 168–198.
- Kaiser, J. (2000). Rift over biodiversity divides ecologists. *Science*, 289, 1282–1283.
- Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *J. Vegetation Sci.*, 3, 157–164.
- Kindscher, K. & Wells, P.V. (1995). Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. *Vegetatio*, 117, 29–50.
- Kinzig, A., Pacala, S.W. & Tilman, D. (2002). *The Functional Consequences of Biodiversity*. Princeton University Press, Princeton, NJ.
- Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.
- Lepš, J., Brown, V.K., Len, T.A.D., Dagmar, G., Hedlund, K., Kailová, J. *et al.* (2001). Separating the chance effect from other diversity effects in the functioning of plant communities. *Oikos*, 92, 123–134.
- Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erseus, C., Ewe, K.C. *et al.* (2001). The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems*, 4, 430–451.
- Littler, M.M. & Littler, D.S. (1995). Impact of CLOD pathogen on Pacific coral reefs. *Science*, 267, 1356–1360.
- Loreau, M. (1994). Material cycling and stability in ecosystems. *Am. Nat.*, 143, 508–513.
- Loreau, M. (1995). Consumers as maximizers of matter and energy flow in ecosystems. *Am. Nat.*, 145, 22–42.
- Loreau, M. (2001). Microbial diversity, producer-decomposer interactions and ecosystem processes: a theoretical model. *Proc. Roy. Soc. London. Ser. B*, 268, 303–309.
- Loreau, M., Downing, A.L., Emmerson, M.C., Gonzalez, A., Hughes, J.B., Inchausti, P. *et al.* (2002a). A new look at the relationship between diversity and stability. In: *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, pp. 79–91.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M., Naeem, S. & Inchausti, P. (2002b). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, Oxford.
- MacArthur, R.H. (1972). *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- May, R.M. (1975). Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.). Belknap Press of Harvard University, Cambridge, MA, pp. 81–120.
- May, R.M. (1995). Conceptual aspects of the quantification of the extent of biological diversity. In: *Biodiversity Measurement and Estimation* (ed. Hawksworth, D.L.). Chapman and Hall, London, pp. 13–20.
- McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.
- McGrady-Steed, J. & Morin, P.J. (2000). Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology*, 81, 361–373.
- Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Högberg, P. & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.*, 2, 237–246.
- Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conserv. Biol.*, 12, 39–45.
- Naeem, S. (2001). Experimental validity and ecological scale as tools for evaluating research programs. In: *Scaling Relationships in Experimental Ecology* (eds Gardner, R.H., Kemp, W.M., Kennedy, V.S. & Petersen, J.E.). Columbia University Press, New York, pp. 223–250.
- Naeem, S. (2002a). Biodiversity equals instability? *Nature*, 416, 23–24.
- Naeem, S. (2002b). Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology*, 83, 2925–2935.
- Naeem, S. (2002c). Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology*, 83, 1537–1552.
- Naeem, S., Byers, D., Tjossem, S.F., Bristow, C. & Li, S. (1999). Plant neighborhood diversity and production. *Ecoscience*, 6, 355–365.
- Naeem, S. & Hawkins, B.A. (1994). Minimal community structure: how parasitoids divide resources. *Ecology*, 75, 79–85.
- Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507–509.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.
- Nijs, I. & Impens, I. (2000). Biological diversity and probability of local extinction of ecosystems. *Funct. Ecol.*, 14, 46–54.
- Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R. & Levin, S. (2001). Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl. Acad. Sci.*, 98, 11376–11381.
- Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.
- Paine, R.T. (2002). Trophic control of production in a rocky intertidal community. *Science*, 296, 736–739.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993). Moose browsing and soil fertility in the boreal forest of Isle Royale National Park. *Ecology*, 74, 467–480.

- Petchey, O.L. & Gaston, K. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.
- Petchy, O.L. & Gaston, K. (2002). Extinction and the loss of functional diversity. *Proc. Roy. Soc. London Ser. B*, 269, 1720–1727.
- Petchy, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72.
- Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent productivity can decrease the stability of ecosystem functioning. *Nature*, 416, 85–86.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, S. *et al.* (1996). Challenges in the quest for keystones. *Bioscience*, 46, 609–620.
- Reaka-Kudla, M.L., Wilson, D.E. & Wilson, E.O. (1997). *Biodiversity II*. Island Press, Washington, DC.
- Reich, P.B., Knops, J., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M. *et al.* (2001). Plant diversity influences ecosystem responses to elevated CO<sub>2</sub> and nitrogen enrichment. *Nature*, 410, 809–812.
- Rosenfeld, J.S. (2002). Logical fallacies in the assessment of functional redundancy. *Conserv. Biol.*, 16, 837–839.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, New York.
- Sankaran, M. & McNaughton, S.J. (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature*, 401, 691–693.
- Schmid, B., Joshi, J. & Schläpfer, F. (2002). Empirical evidence for biodiversity-ecosystem functioning relationships. In: *The Functional Consequences of Biodiversity* (eds Kinzig, A., Pacala, S.W. & Tilman, D.). Princeton University Press, Princeton, NJ.
- Schulze, E.D. & Mooney, H.A. (1993). *Biodiversity and Ecosystem Function*. Springer Verlag, New York.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & van Mantgem, P.J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122, 297–305.
- Smith, T.M., Shugart, H.H. & Woodward, F.I. (1997). *Plant Functional Types*. Cambridge University Press, Cambridge.
- Steneck, R.S. & Watling, L. (1982). Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.*, 68, 299–319.
- Strange, E.M., Fausch, K.D. & Covich, A.P. (1999). Sustaining ecosystem services in human-dominated watersheds: biohydrology and ecosystem processes in the South Platte River Basin. *Environ. Manag.*, 24, 39–54.
- Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *Am. Nat.*, 116, 770–787.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Sieman, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.
- Tilman, D., Lehman, C.L. & Bristow, C.E. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence?. *Am. Nat.*, 151, 277–282.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Tuomisto, H., Ruokolainen, K., Yli-Halla, M. (2003). Dispersal, environment and floristic variation of Western Amazonian forests. *Science*, 299, 241–244.
- Van der Heijden, M.G.A., Klironomas, J.N., Ursic, M., Moutogolia, P., Streitwolf-Engel, R. *et al.* (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69–72.
- Van Minnen, J.G., Leemans, R. & Ihle, F. (2000). Defining the importance of including transient ecosystem responses to simulate C-cycle dynamics in a global change model. *Global Change Biol.*, 6, 595–611.
- Vane-Wright, R.I., Humphries C.J. & Williams P.H. (1991). What to protect? Systematics and the agony of choice. *Biologic. Conserv.*, 55, 235–254.
- Walker, B., Kinzig, A. & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2, 95–113.
- Walker, B.H. (1992). Biological diversity and ecological redundancy. *Conserv. Biol.*, 6, 18–23.
- Wardle, D.A., Bonner, K.I. & Barker, G.M. (2000). Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos*, 89, 11–23.
- Wardle, D.A., Bonner, K.I. & Nicholson, K.S. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, 79, 247–258.
- Warwick, R.M. & Clarke, K.R. (1995). New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Progress Ser.*, 128, 301–305.
- Wellnitz, T. & Poff, N.L. (2001). Functional redundancy in heterogeneous environments: implications for conservation. *Ecol. Lett.*, 4, 177–179.
- Wilsey, B.J. & Polley, H.W. (2002). Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecol. Lett.*, 5, 676–684.
- Wilson, E.O. (1988). *Biodiversity*. National Academy Press, Washington, DC.
- Woodward, F.I. & Diament, A.D. (1991). Functional approaches to predicting ecological effects of global change. *Funct. Ecol.*, 5, 202–212.
- Wright, J.P., Jones, C.G. & Flecker, A.S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132, 96–101.
- Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem functioning in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.*, 96, 1463–1468.
- Zheng, D.W., Bengtsson, J. & Ågren, G.I. (1997). Soil food webs and ecosystem processes: decomposition in donor-control and Lotka-Volterra systems. *Am. Nat.*, 149, 125–148.
- Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin III, F.S., Reynolds, J.F. & Chapin, M.C. (1995). Steppe-tundra transition: herbivore-driven biome shift at the end of the pleistocene. *Am. Nat.*, 146, 765–794.

Manuscript received 6 March 2003

First decision made 15 March 2003

Manuscript accepted 4 April 2003